EVOLUTION OF FLORAL NECTARIES IN IRIDACEAE[1]

Paula J. Rudall,[2] John C. Manning,[3] and Peter Goldblatt[4]

ABSTRACT

New data on nectaries in Iridaceae are presented in combination with a literature review, in the context of systematics and pollination biology. Iridaceae are a highly diverse family with respect to nectar production, reflecting the wide range of pollination syndromes within the family. Based on outgroup comparison, presence of septal nectaries is probably the plesiomorphic condition for Iridaceae, despite their absence from the putatively basal genus *Isophysis*. Within Iridaceae, septal nectaries are present in the largest subfamily Crocoideae (Ixioideae) and also in *Diplarrhena*, which is putatively sister to all other Iridoideae, but absent from the rest of Iridoideae. Within the paraphyletic Nivenioideae (six genera), septal nectaries are absent from *Aristea*, *Geosiris*, and *Patersonia* and present in the three shrubby Cape genera *Klattia*, *Nivenia*, and *Witsenia*. Perigonal nectaries and elaiophores (oil-producing hairs) are mostly confined to the subfamily Iridoideae, where they take many different forms, although some Iridoideae lack nectaries entirely. In different species of *Iris*, nectaries are present either on the base of the perianth tube or around the base of the style, or sometimes in a continuous region between the two. In many other Irideae they are located at the bases of the outer tepals (most species of *Moraea*) or the bases of all six tepals (e.g., *Ferraria*). In *Olsynium douglasii* and *O. junceum* (Sisyrinchieae) nectar is apparently secreted directly from the filament column, and in *Sisyrinchium* subg. *Sisyrinchium* elaiophores are present on the lower part of the filament column. Perigonal nectaries may have evolved from septal nectaries by developmentally later formation of nectaries in a more distal position on organ primordia (i.e., heterochrony).

Key words: *Diplarrhena*, epigyny, heterochrony, *Isophysis*, perigonal nectary, septal nectary, systematics.

Iridaceae are a cosmopolitan family comprising about 65 genera and 1850 species that are most abundant and diverse in the Southern Hemisphere, especially Africa. They represent an unusually coherent family among lilioid monocots, possessing several reliable morphological synapomorphies, including the presence of isobilateral unifacial leaves, styloid crystals, and flowers with only three stamens (i.e., lacking the inner staminal whorl). Recent molecular analyses of monocotyledons (e.g., Chase et al., 1995, 2000) have consistently placed Iridaceae in the order Asparagales, among the lower asparagoid grade, associated with families such as Doryanthaceae (*Doryanthes*), Ixioliriaceae (*Ixiolirion*), and Tecophilaeaceae. Iridaceae and Orchidaceae represent easily the largest families of Asparagales (indeed, orchids are arguably the second-largest angiosperm family). Despite their readily diagnostic features, both families are unusually diverse in terms of morphological features, and both share some characters with the order Liliales, including the presence of perigonal nectaries in some taxa. For this reason they were formerly thought (e.g., by Dahlgren & Clifford, 1982; Dahlgren et al., 1985) to be closely related to some families of Liliales, although molecular analyses have now clarified their placement in Asparagales (APG, 1998).

Septal nectaries are a characteristic feature of flowers of many monocotyledons (Van Heel, 1988; Schmid, 1985, 1988; Endress, 1995; Simpson, 1993, 1998; Smets et al., 2000). They result from incomplete fusion of a small region of the carpel margins, which are otherwise fused. In contrast, perigonal (stamen and tepal) nectaries occur mainly in the orders Asparagales and Liliales, but are concentrated in Liliales, where septal nectaries are entirely absent (Rudall et al., 2000). Septal nectaries and perigonal nectaries rarely (or possibly never) occur together in the same flower in monocots (Smets et al., 2000). Iridaceae are highly unusual (possibly unique) in that both types occur in different genera within the family, some members of which also have oil-producing epidermal cells and trichomes (elaiophores), all probably related to different pollination syndromes. This paper reviews

Crocoideae (+sn)

Nivenieae (+sn)

Aristea (-sn)

Geosiris (-sn)

Patersonia (-sn)

} Nivenioideae

Mariceae (-sn)

Tigridieae (-sn)

Sisyrinchieae (-sn)

Irideae1 (-sn)

Bobartia (-sn)

Irideae2 (-sn)

Diplarrhena (+sn)

} Iridoideae

Isophysis (-sn)

Tecophilaeaceae (+/-sn)

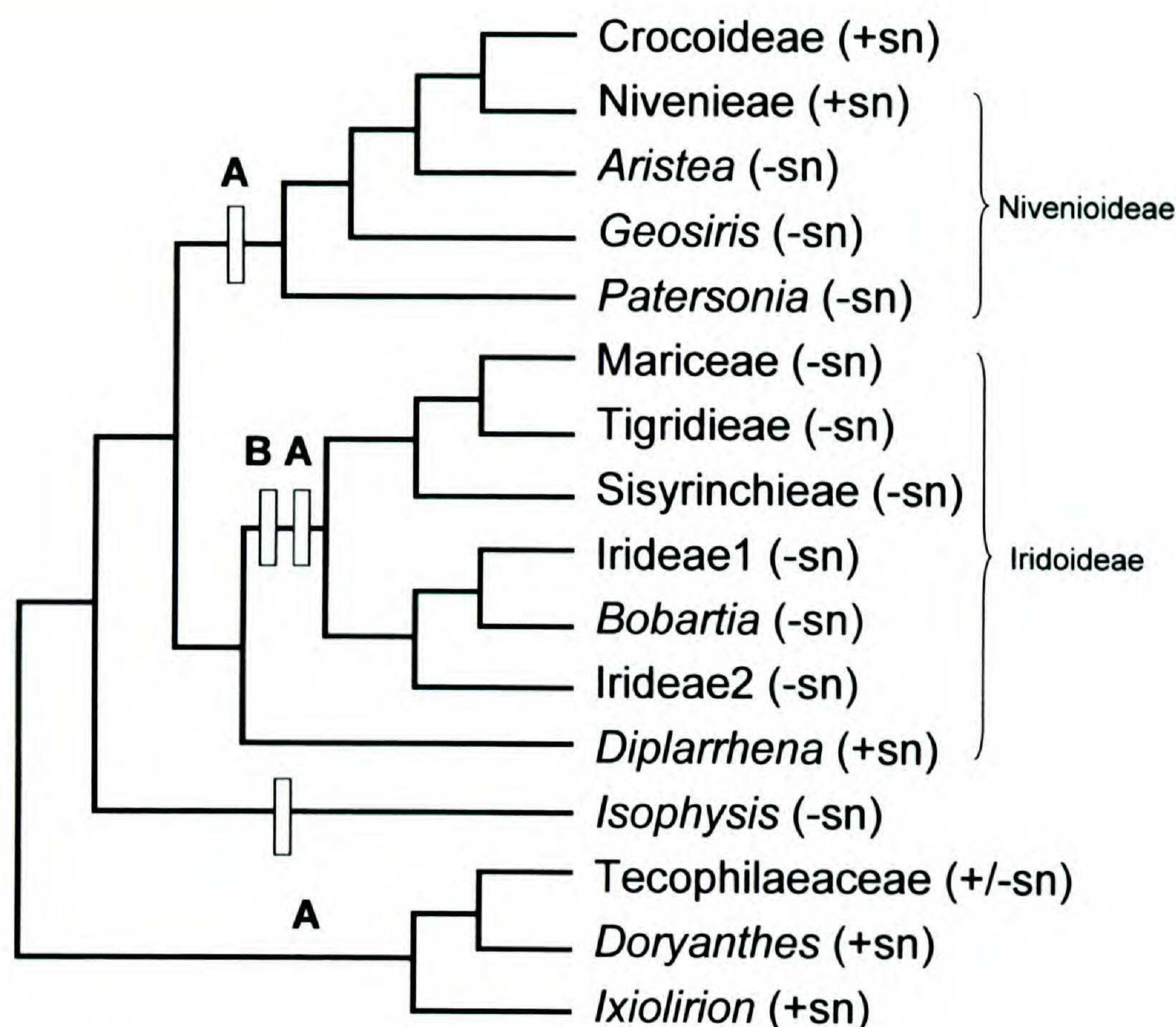*Doryanthes* (+sn)

Ixiolirion (+sn)

A   B A   A

Figure 1.   Diagram of relationships in Iridaceae, based on a combined molecular tree presented by Reeves et al. (2001), showing characters optimized. A = loss of septal nectaries (i.e., complete fusion of carpel margins); B = perigonal nectaries present (not in all taxa); sn = septal nectaries. An equally parsimonious option would be loss of septal nectaries on the branch leading to Iridaceae, with at least two subsequent regains (but see discussion).

the distribution of these characters in a systematic context, in order to assess their evolution within Iridaceae. Particular reference is made to a recent combined molecular analysis of Iridaceae using four plastid DNA data sets (two protein coding genes: rps4, rbcL, the trnL intron, and the trnL-F inter-gene spacer: Reeves et al., 2001; Fig. 1).

MATERIALS AND METHODS

Material examined was taken from sources indicated in Table 1. Flowers were fixed in FAA (formalin acetic alcohol) and stored in 70% ethanol before processing. Flowers were embedded in Paraplast using standard methods of wax embedding and serially sectioned using a rotary microtome. Paraffin sections were stained with safranin O and Alcian blue 8GX, dehydrated through an alcohol series to 100% ethanol then Histoclear, mounted in Euparal or DPX mountant, and examined using normal bright-field optics.

RESULTS

The systematic distribution of nectaries in Iridaceae is summarized in Table 2 using the classification of Goldblatt (1990, 1998a). Within the larg-

est subfamily Crocoideae (Ixioideae, including ca. 28 genera of Africa and Eurasia), septal nectaries are present in representative species of all genera examined (Tables 1, 2; Daumann, 1970; de Vos, 1974a, b, 1982, 1984, 1985) (Figs. 1A, B, 5C, 6A, C). The so-called stylar nectaries described by Daumann (1970) for *Lapeirousia laxa* (Thunb.) N. E. Br. and *L. cruenta* (Lindl.) Baker (= *Freesia laxa* (Thunb.) Goldblatt & J. C. Manning: Goldblatt & Manning, 1995) are probably septal nectaries with pores opening close to the base of the style. Nectar production is suppressed in some Crocoideae, notably *Ixia* subg. *Ixia* (Goldblatt et al., 2000a), but non-functional septal nectaries are apparently present in these taxa, for example, in *I. maculata* L. and *I. viridiflora* (Daumann, 1970).

Septal nectaries are also present in *Diplarrhena* (Fig. 5B) but absent from all other members of subfamily Iridoideae (sensu Goldblatt, 1998a) examined here (Figs. 2C, D, F, 3E, 5A, 6B, 7A, 8A). Within subfamily Nivenioideae, which includes six genera (Goldblatt, 1998a), septal nectaries are absent from *Aristea* (Fig. 4B), *Geosiris* (Fig. 4C), and *Patersonia*, and nectar is not produced in most *Aristea* species (but see below). However, septal nectaries are present in the shrubby Cape genera *Klat-*

Table 1. List of species examined, with sources of plant material. For Iridaceae classification used here, see Goldblatt (1990, 1998a).

Taxon	Collection data
Subfamily Isophysidoideae	
Isophysis tasmanica (Hook.) T. Moore	Australia, Tasmania, *Jarman s.n.* (MO)
Subfamily Nivenioideae	
Aristea ecklonii Baker	Cultivated material, NBG Kirstenbosch, South Africa
Aristea ecklonii Baker	Cultivated material, RBG Kew, U.K.
Geosiris madagascariensis Baill.	Madagascar, *Dorr et al. s.n.* (MO)
Klattia stokoei L. Guthrie	South Africa, W. Cape, *Goldblatt 8347* (MO)
Klattia flava (G. J. Lewis) Goldblatt	South Africa, W. Cape, *Goldblatt 8656* (MO)
Nivenia binata Klatt	South Africa, W. Cape, *Goldblatt 7959* (MO)
Nivenia stokoei (L. Guthrie) N. E. Br.	South Africa, W. Cape, *Goldblatt 7628* (MO)
Patersonia longifolia R. Br.	Australia, New South Wales, *Ladd s.n.* (NBG)
Witsenia maura (L.) Thunb.	South Africa, W. Cape, *Goldblatt & Gentry 1600* (NBG)
Subfamily Iridoideae	
Tribe Diplarrheneae	
Diplarrhena latifolia Benth.	Cultivated material, RBG Kew, U.K. (1980–2283)
Tribe Sisyrinchieae	
Libertia grandiflora Sweet	Cultivated material, RBG Kew, U.K.
Olsynium douglasii A. Dietr.	U.S.A., Washington, *Goldblatt 11642* (MO)
Olsynium junceum (E. Mey. ex Presl) Goldblatt	Cultivated material, RBG Kew, U.K.
Orthrosanthus laxus (Endl.) Benth.	Cultivated material, RBG Melbourne, Australia
Orthrosanthus sp.	Cultivated material, RBG Kew, U.K.
Sisyrinchium striatum Sm.	Cultivated material, RBG Kew, U.K.
Sisyrinchium sp.	Cultivated material, RBG Kew, U.K.
Tribe Irideae	
Belamcanda chinensis (L.) DC.	Cultivated material, University of Durban-Westville, S. Africa
Bobartia gladiata (L.f.) Ker-Gawl.	South Africa, W. Cape, *Boucher 5263* (NBG)
Dietes grandiflora N. E. Br.	Cultivated material, NBG Kirstenbosch, South Africa
Ferraria crispa Burm.	South Africa, W. Cape, *Goldblatt & Manning 11665* (MO)
Ferraria foliosa G. J. Lewis	South Africa, W. Cape, *Goldblatt & Porter 11888* (MO)
Ferraria ferrariola (Jacq.) Willd.	South Africa, N. Cape, *Goldblatt & Porter 11765* (MO)
Ferraria divaricata Sweet subsp. *divaricata*	South Africa, N. Cape, *Goldblatt & Manning 10176* (MO)
Ferraria schaeferi Dinter	South Africa, W. Cape, *Goldblatt & Porter 11734* (MO)
Moraea collina Thunb.	South Africa, W. Cape, *Goldblatt 2132* (MO, NBG)
Moraea spathulata (L.f.) Klatt	South Africa, E. Cape, *Goldblatt 12232* (MO)
Tribe Tigridieae	
Alophia drummondii (Graham) R. C. Foster	Cultivated material, Missouri BG, U.S.A.
Ennealophus euryandrus (Griseb.) P. Ravenna	Cultivated material, RBG Kew, U.K.
Gelasine elongata (R. Grah.) P. Ravenna	Cultivated material, ex hort. B. Mathew, Surrey, U.K.
Tigridia meleagris (Lindl.) Nichols.	Mexico, Kenton, *Rudall & Howard 49-319* (K)
Tribe Trimezieae	
Pseudotrimezia planifolia P. Ravenna	Brazil, *Harley et al. 25445* (K)
Subfamily Crocoideae (Ixioideae)	
Tribe Pillansieae	
Pillansia templemannii L. Bolus	South Africa, W. Cape, *Goldblatt 7907A* (MO, NBG)

Table 1. Continued.

Taxon	Collection data
Tribe Watsonieae	
Lapeirousia neglecta Goldblatt & J. C. Manning	South Africa, W. Cape, *Goldblatt & Manning 9022* (MO)
Micranthus alopecuroides (L.) Rothm.	South Africa, *Goldblatt & Manning 10431* (NBG)
Thereianthus racemosus (Klaff) G. J. Lewis	South Africa, W. Cape, *Manning s.n.* (NBG)
Watsonia angusta Ker-Gawl.	South Africa, W. Cape, *Snijman 971* (NBG)
Tribe Ixieae	
Babiana sinuata G. J. Lewis	South Africa, W. Cape, *Goldblatt 2545* (MO, NBG)
B. stricta (Aiton) Ker-Gawl.	South Africa, W. Cape, *Goldblatt & Manning 10343* (NBG)
Crocus sieberi Gay	Cultivated material, RBG, Kew, U.K.
Dierama pendulum (L. f.) Walp.	Cultivated material, NBG Kirstenbosch, South Africa
Freesia alba (G. L. Meyer) Gumbleton	Cultivated material, NBG Kirstenbosch, South Africa
F. grandiflora (Baker) Klaff	Cultivated material, NBG Kirstenbosch, South Africa
Geissorhiza ornithogaloides Klatt	South Africa, W. Cape, *Manning 2026* (NBG)
Gladiolus gracilis Jacq.	South Africa, W. Cape, *Manning 2016* (NBG)
Hesperantha falcata (L. f.) Ker-Gawl.	South Africa, near George, *Goldblatt & Manning s.n.*
Ixia polystachya L.	South Africa, ex hort. Kirstenbosch
Melasphaerula ramosa (Burm. f.) N. E. Br.	South Africa, W. Cape, Cape Peninsula, *Goldblatt & Manning s.n.*
Romulea rosea (L.) Eckl.	South Africa, W. Cape, *Manning 2017* (NBG)
Sparaxis grandiflora (D. Delaroche) Ker-Gawl.	Cultivated material, NBG Kirstenbosch, South Africa
Tritonia squalida (Aiton) Ker-Gawl.	South Africa, W. Cape, near Albertinia, *Goldblatt & Manning s.n.*
Tritoniopsis parviflora (Jacq.) G. J. Lewis	South Africa, *Goldblatt & Manning 2283* (NBG)
Tritoniopsis burchellii (N. E. Br.) Goldblatt	South Africa, W. Cape, *Goldblatt & Manning 9869* (NBG)
Xenoscapa fistulosa (E. Mey. ex Klaff) Goldblatt	South Africa, W. Cape, *Manning 2028* (NBG)

tia, Nivenia, and *Witsenia* (Figs. 3A, F, G, 4D, E), which together form a clade (Manning & Goldblatt, 1991; Reeves et al., 2001). Septal nectaries are absent from the monogeneric subfamily Isophysidoideae (*Isophysis*) (Fig. 2E).

Perigonal nectaries and elaiophores (oil-producing hairs) are mostly confined to subfamily Iridoideae, in which septal nectaries are always absent (except *Diplarrhena*; see above). However, there are at least two examples of perigonal nectaries or elaiophores in taxa outside Iridoideae: (1) one species of Nivenioideae (*Aristea spiralis* (L.f.) Ker-Gawl.) produces nectar that is secreted from small perigonal nectaries on the short perianth tube below the base of the free parts of the tepals (Fig. 4A); Daumann (1970) also reported perigonal nectaries in *A. africana* (L.) Hoffmanns. (2) In *Tritoniopsis parviflora* (Jacq.) G. J. Lewis (subfamily Crocoideae), floral oils are produced from a glandular epithelium at the base of the free parts of the tepals and in the mouth of the perianth tube (Manning & Goldblatt, 2002). Oil secretion is supplemented by production of sugary nectar from septal nectaries.

Within subfamily Iridoideae, perigonal nectaries and elaiophores take several different forms. Daumann (1935) illustrated highly vascularized nectariferous regions present on different parts of the flower surface in different species of *Iris*. These included:

(1) Nectaries present on the base of the perianth tube (comprising fused perianth and staminal tissue), especially (but not exclusively) in the interstaminal regions (e.g., in *I. douglasiana* Torr., *I. ensata* Thunb., *I. foetidissima* L., *I. graminea* L., *I. pseudacorus* L., *I. sibirica* L., and also in two allied monotypic genera, *Belamcanda* and *Hermodactylis*).

(2) Nectaries present around the base of the style (e.g., in *I. dichotoma* Pall.).

(3) Nectaries present in a continuous region extending from around the base of the perianth tube to around the base of the style (e.g., in *I. chamaeiris* Bertol., *I. germanica* L., *I. kolpakowskiana* Regel, *I. pumila* L., *I. stolonifera* Maxim., *I. tectorum* Maxim., *I. tingitana* Boiss. & Reut., *I. warleyensis* Foster, *I. xiphioides* Ehrh.) extending onto the bases of the inner tepals in *I. sisyrinchium* L. These are not

Table 2.   Distribution of nectaries in Iridaceae (arranged according to the classification of Goldblatt, 1990, 1998a).

Taxon	Septal nectaries	Other floral secretory structures
Isophysidoideae (*Isophysis*)	absent (Fig. 5A)	absent
Nivenioideae	absent from *Aristea* (Fig. 4B), *Geosiris* (fig. 4C), *Patersonia*, present in *Klattia*, *Nivenia* (Fig. 3F, G), *Witsenia* (Fig. 4D, E)	absent, except in *Aristea spiralis*, in which small perigonal nectaries present (Fig. 4A)
Iridoideae	absent (except in *Diplarrhena*: Fig. 5B)	often present
Bobartia	absent (Fig. 5A)	absent
Dietes	absent (Fig. 6B)	absent
Diplarrhena	present (Fig. 5B)	absent
Iridoideae–Sisyrinchieae	absent (Figs. 2C, D, 3E, 7A, 8A)	nectar secreted from filament column in *Olsynium* (Figs. 7, 8); elaiophores present on filament column in many species of *Sisyrinchium* subg. *Sisyrinchium* (Fig. 3C–E)
Iridoideae–Irideae	absent (Figs. 5A, 6B)	perigonal nectaries present in *Moraea* (Fig. 6D) and *Ferraria*, or on the walls of the perianth tube in *Iris*
Iridoideae–Tigridieae	absent (Fig. 2F)	elaiphores present on tepal claws in some species (Figs. 3B, 9)
Iridoideae–Trimezieae	absent	elaiophores present on tepal claws in some species
Crocoideae	present in all taxa (Figs. 2A, B, 5C, 6A, C)	absent

septal nectaries, because they do not extend into the unfused regions of the carpel margins within the ovary, but they could easily be mistakenly identified as such in the absence of anatomical sections.

Among other members of the Old World and North American tribe Irideae, in *Moraea* and *Ferraria* the smooth glistening perigonal nectaries, when present, can readily be seen with the naked eye; they are located at the bases of the outer tepals (in most species of *Moraea*) or at or near the bases of all six tepals (in *Ferraria* and many *Moraea* spp.) (Vogel, 1954; Daumann, 1970; de Vos, 1979; Goldblatt, 1986, 1987; Goldblatt & Manning, unpublished data). In some species of *Ferraria* the nectaries may cover more than half the area of the tepal claws and measure up to 4 × 3 mm. Species of *Dietes* and *Bobartia* apparently lack nectaries entirely (Figs. 5A, 6B) and produce no nectar, as indicated by visual observation and the taste test (applying likely nectar-bearing parts of the flower to the tongue) (Goldblatt, unpublished data). This observation refutes Daumann's (1970) reports of perigonal nectaries in *Dietes bicolor* (Lindl.) Sweet and *D. iridoides* (L.) Sweet ex Klatt (as both *D. vegeta* (L.) N. E. Br. and *Moraea iridoides* L.). In *Moraea ochroleuca* (Salisb.) Drapiez and *M. lurida* Ker-Gawl. nectar is produced along the length of all six tepal claws above the vascular strands but no nec-

tariferous glands are evident (Goldblatt et al., 1998; Goldblatt & Manning, 2002). Nectaries are not developed in several species of *Moraea* that are pollinated by hopliine scarab beetles, e.g., *M. cantharophila* Goldblatt & J. C. Manning, *M. tulbaghensis* L. Bolus, and *M. villosa* Ker-Gawl. (Goldblatt et al., 1998; Goldblatt & Manning, 2002; Steiner, 1998).

The New World Iridoideae are currently distributed among tribes Sisyrinchieae, Trimezieae, and Tigrideae (Goldblatt, 1990, 1998a). These include numerous species that produce nectar from various different parts of the flower, although some apparently lack nectar entirely; for example, Cocucci and Vogel (2001) reported that *Olsynium philippi* (Klatt) Goldblatt (Sisyrinchieae) does not produce nectar. In many Iridoideae (and other Iridaceae) the stamen filaments are free in the upper half and fused into a filament column at their base. In *O. douglasii* A. Dietr. the outer surface of the filament column is smooth, with large epidermal cells and dark-staining highly vascularized tissue beneath, indicating a nectary (Fig. 7A–D). The inner surface of the filament column is highly convoluted and thin-walled. The filament column is swollen just above the base; nectar presumably accumulates in a subepidermal space in this region. After exudation, nectar then accumulates in a semi-enclosed cham-
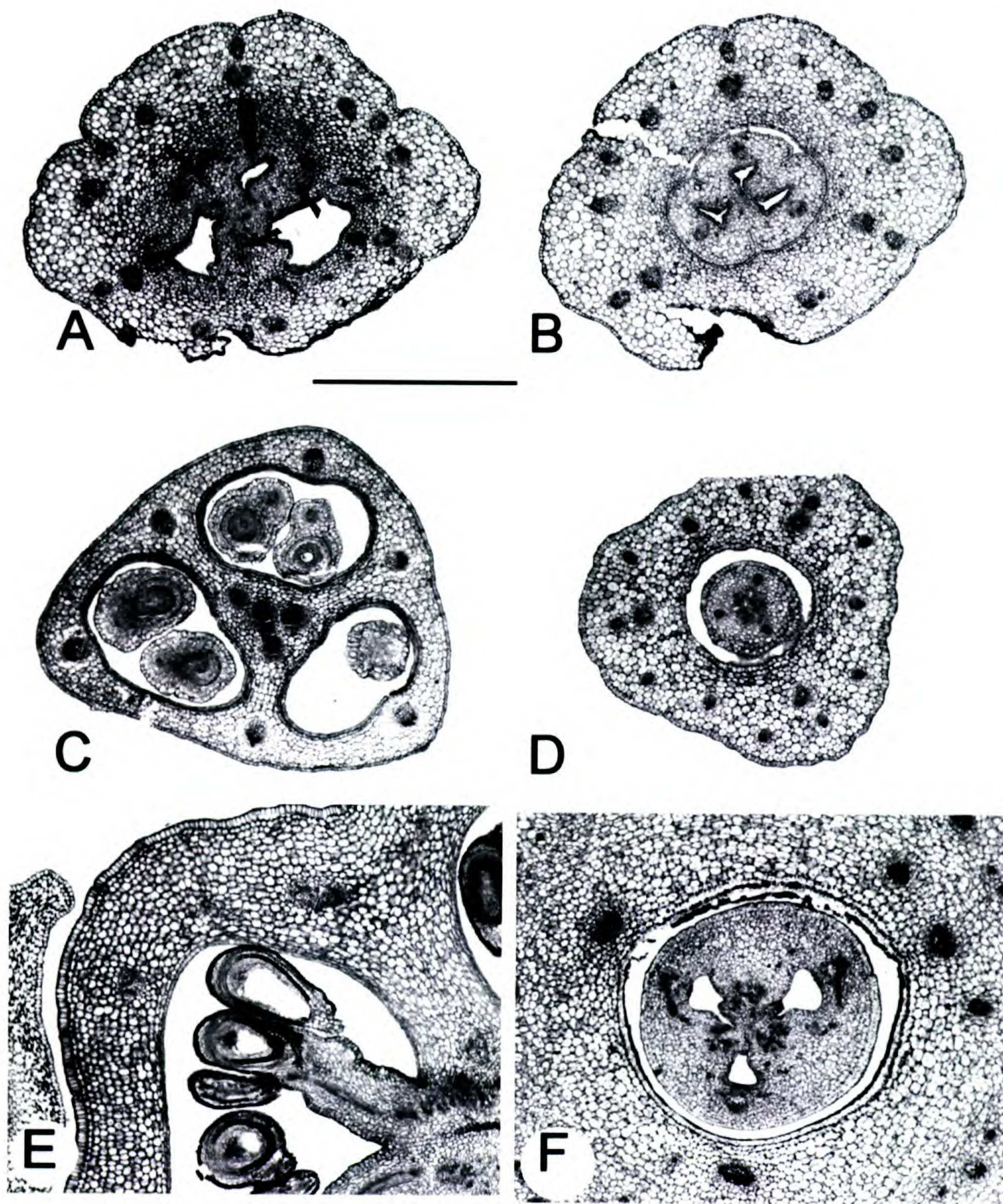
Figure 2.   —A, B. *Crocus sieberi* (Crocoideae), transverse sections (TS) of flower through base of ovary (A) and top of ovary (B); septal nectaries arrowed. —C, D. *Orthrosanthus laxus* (Iridoideae–Sisyrinchieae), TS of flower through ovary (C) and style plus perianth tube (D); nectaries absent. —E. *Isophysis tasmanica* (Isophysidoideae), TS of superior ovary; nectaries absent. —F. *Gelasine elongata* (Iridoideae–Tigridieae), TS of top of ovary, nectaries absent. Scale = 0.5 mm for all images.

ber around the narrow basal part of the column. This nectar chamber (also present in some *Moraea* species, e.g., *M. miniata* Andr.; Goldblatt & Bernhardt, 1999) is enclosed by the short perianth tube (in *Olsynium*), the walls of which are almost in contact with the swollen portion of the filament column, or by the short tepal claws that abut the swollen lower portion of the filament column (in *Moraea*). Other species of *Olsynium* have a similar swollen

base to the filament column and a perianth tube and most likely also produce nectar in the manner described for *O. douglasii*. At least *O. junceum* (E. Mey. ex Presl) Goldblatt is known to produce nectar (Forcone et al., 1998), which is presumably secreted from anticlinally elongated epidermal cells on both surfaces of the filament tube (Fig. 8).

Many other New World Iridoideae bear trichome elaiophores, which are invariably unicellular and
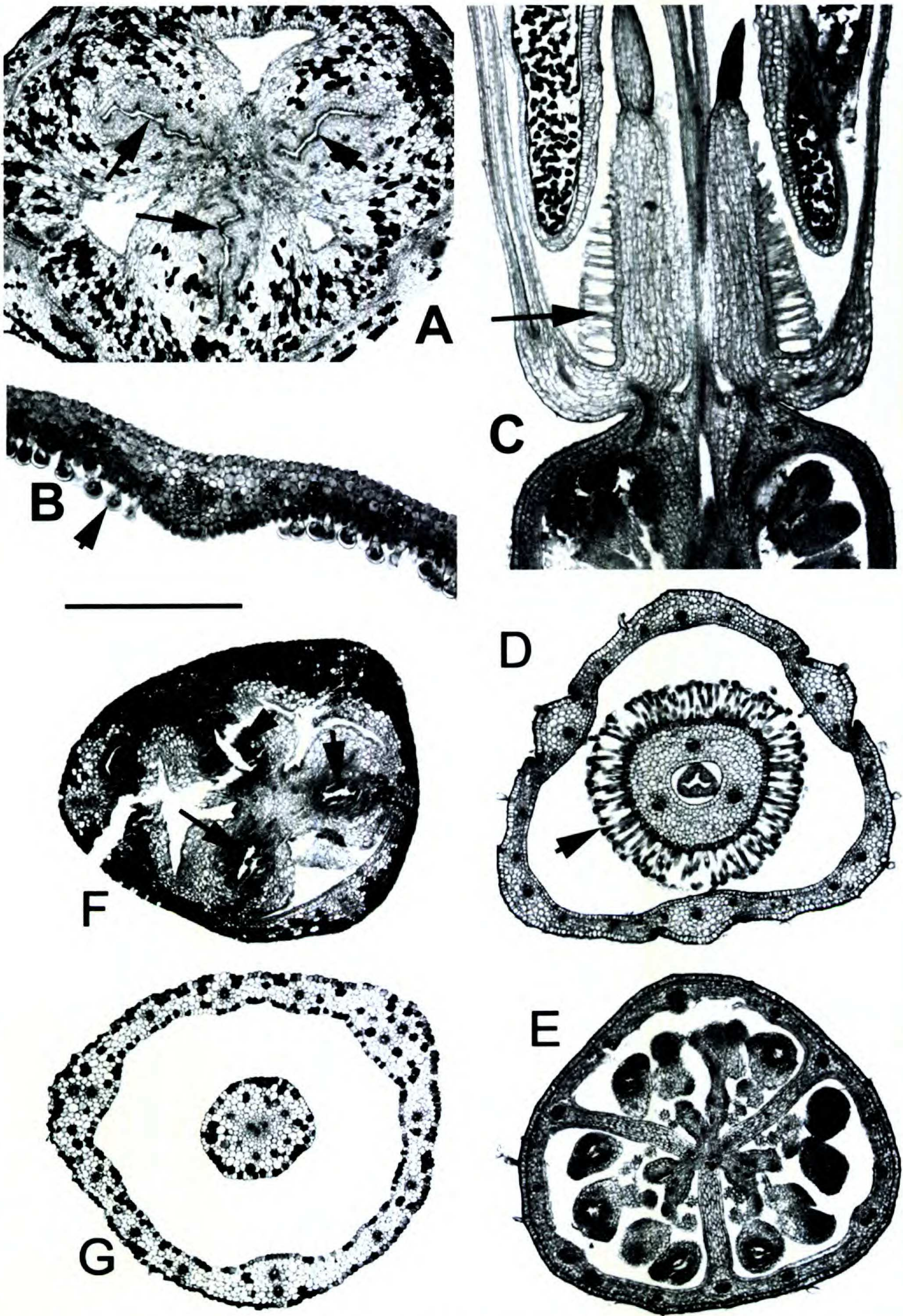
Figure 3. —A. *Klattia stokoei* (Nivenioideae), TS of flower just proximal to top of semi-inferior ovary, showing septal nectaries (arrowed). —B. *Tigridia meleagris* (Iridoideae–Tigridieae), TS of inner tepal with oil-producing trichomes (elaiophores). C–E. *Sisyrinchium* sp. (Iridoideae–Sisyrinchieae). —C. Longitudinal section (LS) of flower showing distal end of inferior ovary and proximal end of perianth tube, staminal column, and central style, with elaiophores present on staminal column. —D. TS of staminal column (with elaiophores) and central style. —E. TS of ovary, lacking septal nectaries. F, G. *Nivenia binata* (Nivenioideae). —F. TS of flower just proximal to top of semi-inferior ovary, showing septal nectaries (arrowed). —G. TS of perianth/stamen tube and style. Scale = 0.5 mm for all images.
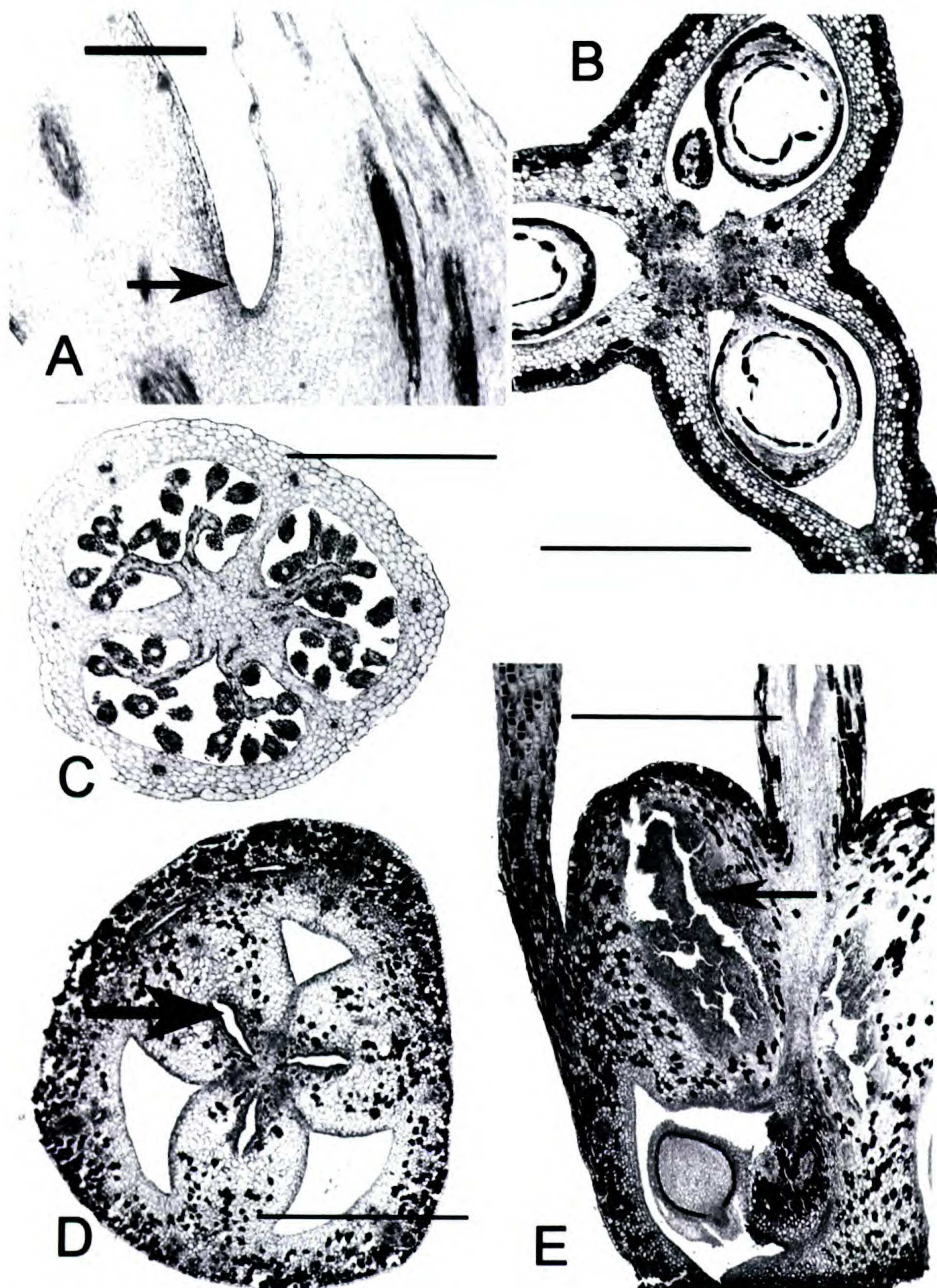
Figure 4. —A. *Aristea spiralis* (Nivenioideae), LS of top of ovary with perigonal nectary at base of perianth tube arrowed. —B. *Aristea ecklonii* (Nivenioideae), TS of ovary, lacking septal nectaries. —C. *Geosiris madagascariensis* (Nivenioideae), TS of ovary, lacking septal nectaries. D, E, *Witsenia maura* (Nivenioideae). —D. TS of top part of ovary, with one of three septal nectaries arrowed. —E. LS of ovary, with one of three septal nectaries arrowed. Scales: in A = 100 μm; in B–E = 0.5 mm.

club-shaped, with a rounded tip. In *Sisyrinchium* subg. *Sisyrinchium* trichomes (elaiophores) present on the lower part of the filament column (Fig. 3C, D) secrete floral oils; this was first reported by Vogel (1971, 1974) and described in detail by Cocucci and Vogel (2001). Similar trichome elaio-

phores also occur on the tepal claws in Tigridieae, including *Alophia* (syn. *Eustylis*), *Cypella*, *Ennealophus* (Fig. 9), *Fosteria* (a genus closely allied to, if not nested in *Tigridia*: Goldblatt, 1998a), *Gelasine*, *Herbertia*, many species of *Tigridia* (Fig. 3B), and Trimezieae, including *Neomarica* (Molseed,
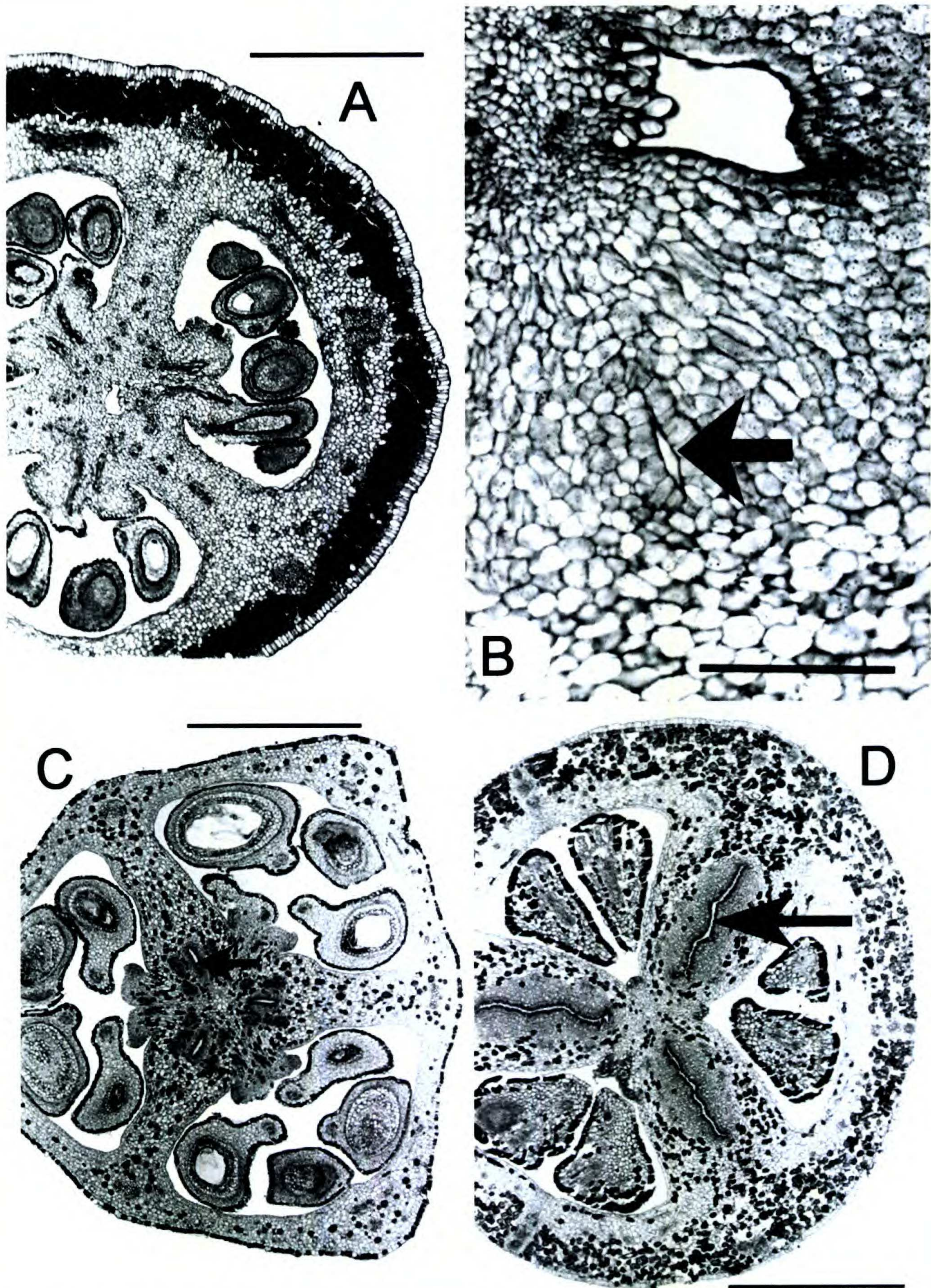
Figure 5.   —A. *Bobartia gladiata* (Iridoideae–Irideae), TS of ovary, lacking septal nectaries. —B. *Diplarrhena latifolia* (Iridoideae–Diplarrheneae), TS of septal nectary (arrowed). —C. *Babiana stricta* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. —D. *Tritoniopsis burchellii* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. Scales: in A, C, D = 0.5 mm; in B = 100 μm.
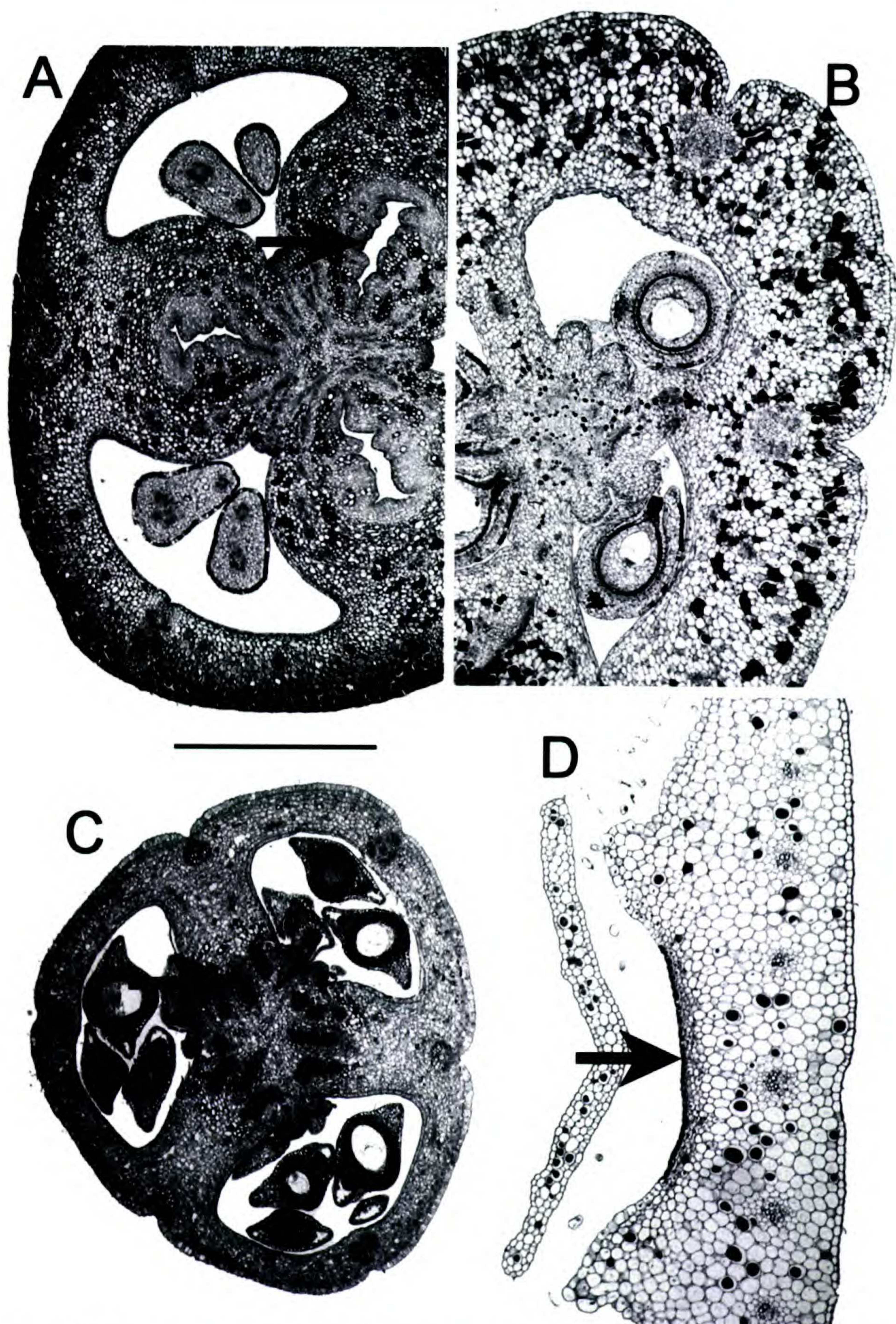
Figure 6.   —A. *Watsonia angusta* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. —B. *Dietes grandiflora* (Iridoideae–Irideae), TS of ovary, lacking septal nectaries. —C. *Gladiolus gracilis* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. —D. *Moraea spathulata* (Iridoideae–Irideae), TS of tepals, with perigonal nectary arrowed. Scale = 0.5 mm.
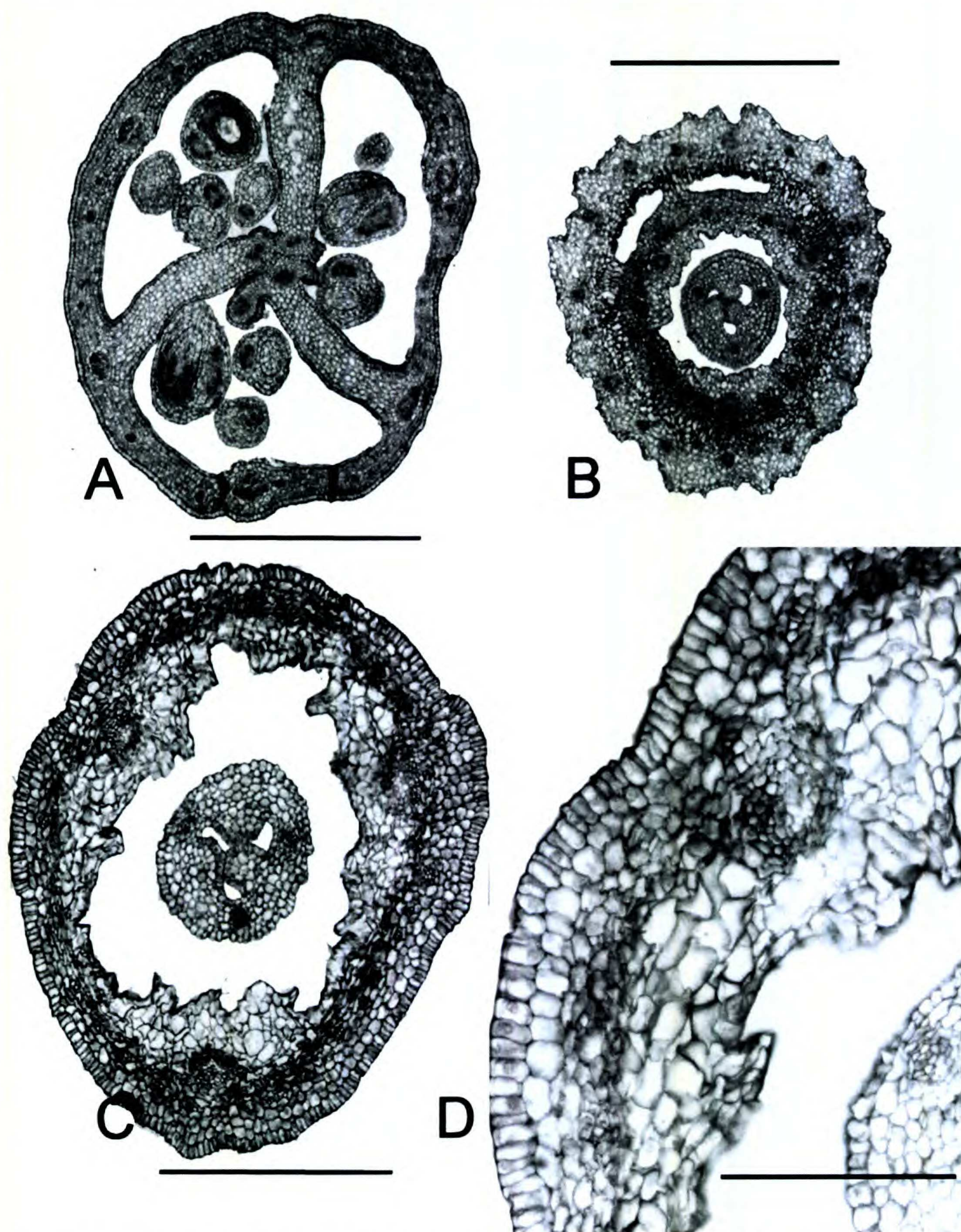
Figure 7. *Olsynium douglasii* (Iridoideae–Sisyrinchieae), serial TS of flower. —A. TS of ovary, lacking septal nectaries. —B. Just above top of inferior ovary, showing central style surrounded by staminal column partially fused with perianth tube. —C. More distal section showing central style surrounded by staminal column in which the outer epidermal cells are axially elongated and the inner epidermis is thin-walled and convoluted. —D. Enlarged view of part of staminal column showing extensive vascular tissue beneath outer epidermis. Scales: in A–C = 0.5 mm; in D = 100 μm.
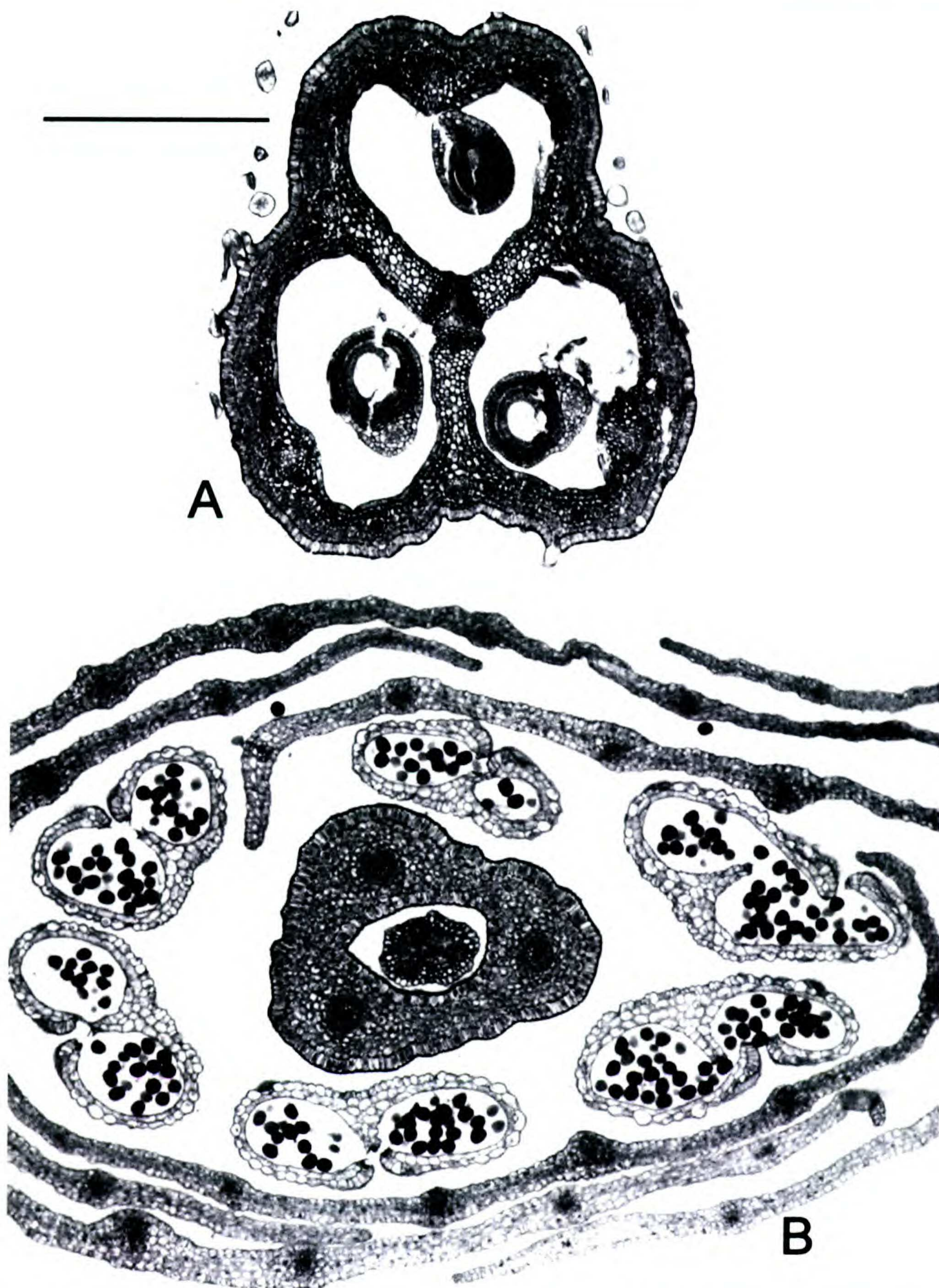
Figure 8. *Olsynium junceum* (Iridoideae–Sisyrinchieae), TS of flower. —A. TS of ovary, lacking septal nectaries. —B. TS above top of inferior ovary, showing central style surrounded by staminal column in which both outer and inner epidermal cells are axially elongated. Scale = 0.5 mm.

1968, 1970; Vogel, 1974; Lee, 1994). The elaiophores develop from epidermal cells rather late in development, shortly prior to anthesis. Their distribution on the tepals varies, although in general the zone of glandular trichomes is restricted to the adaxial surfaces of the smaller inner tepals, often concentrated in pouches at the juncture of the tepal claw and limb. In *Herbertia* there are nectaries on

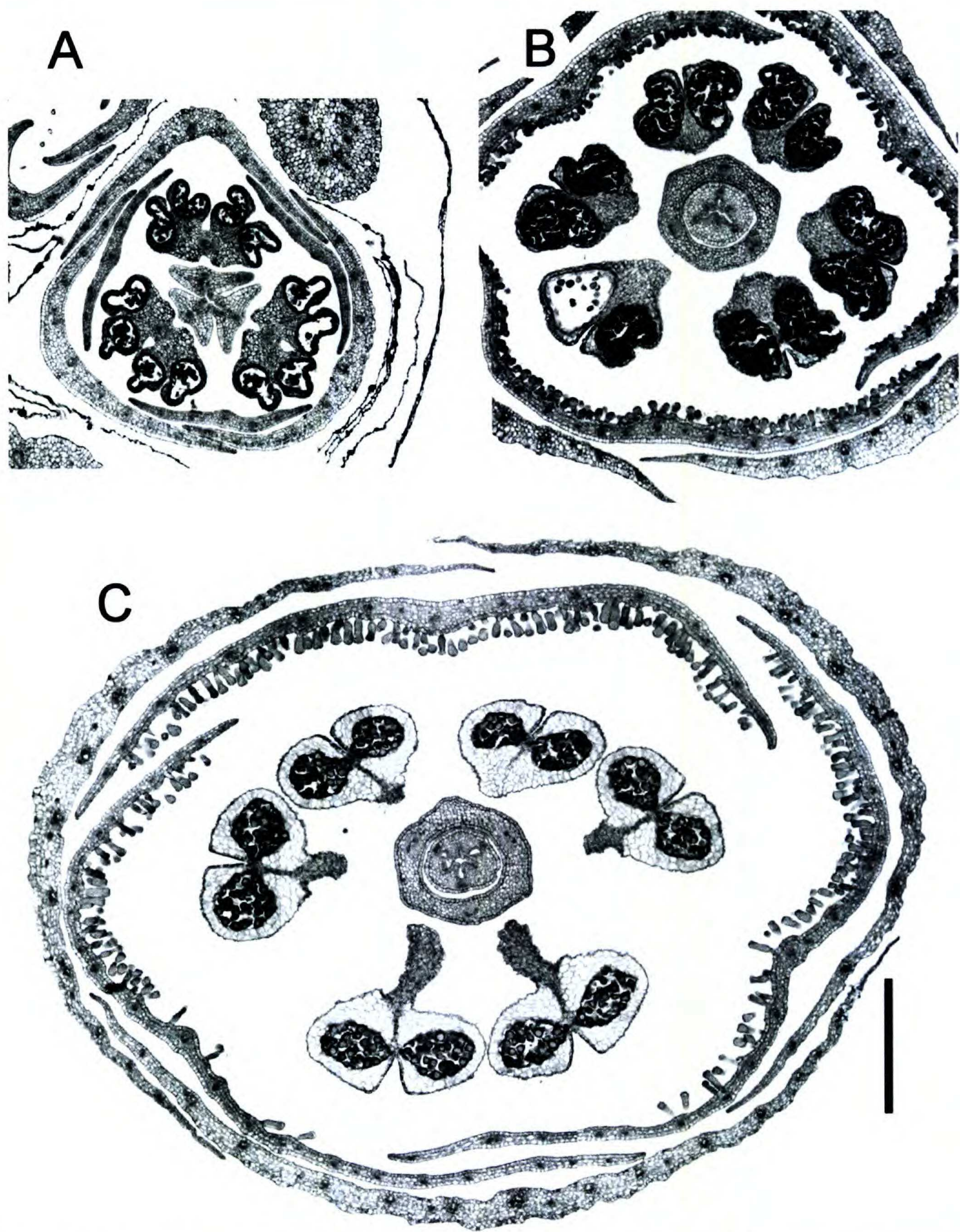Figure 9. *Ennealophus euryandrus* (Iridoideae–Tigridieae), TS of flowers through style. —A. TS of young bud; perigonal trichomes not developed. —B. TS of older bud; short perigonal trichomes (elaiophores) present on inner surface of inner tepals. —C. TS of bud just before anthesis; longer trichomes (elaiophores) present on inner surface of inner tepals. Scale = 0.5 mm.

the smaller inner tepals and the claws of the outer tepals. At least two genera of the tribe apparently lack nectaries: *Sessilanthera* and *Cobana*, which have porose anthers and on this basis are expected to be buzz pollinated. Absence of nectar is often associated with buzz pollination, and information available indicates that these two genera lack nectaries and elaiophores (Molseed & Cruden, 1969; Ravenna, 1974). *Eleutherine* and *Nemastylis* also evidently lack nectaries (Molseed, 1970) but these species have conventional longitudinal anther dehiscence.

Red-flowered and presumably hummingbird-pollinated species of *Tigridia*, which were formerly placed in a separate genus, *Rigidella* (Goldblatt, 1998a), secrete copious amounts of sugary nectar from nectaries on the inner tepal claws (Cruden, 1971). Other Tigridieae may also secrete nectar from perigonal nectaries, although this is not adequately documented. Molseed (1970) mentioned fly and wasp visitors in some small-flowered species of *Tigridia*; as far as we know flies and wasps do not take floral oils as a reward.

Lee (1994) described a novel mode of nectar production in *Alophia drummondii* Grah. in which the expanded, fiddle-shaped anther connectives secrete a sticky mucilage with dilute sugar content. During the later stages of anthesis this is concentrated by evaporation to form an alternative nectar source. The primary role of the mucilage is reportedly to promote pollen adherence on the dorsal thorax of visiting bees.

DISCUSSION

SEPTAL NECTARIES IN ASPARAGALES

An understanding of sister-group relationships is critical for optimization of characters onto an existing phylogeny. However, this is problematical for Iridaceae because relationships among the various lower asparagoid clades are still not satisfactorily resolved, partly because *Ixiolirion* is a "wildcard" taxon on a very long branch in molecular analyses (Fay et al., 2000), tending to destabilize tree topology. Three taxa, *Ixiolirion* (Ixioliriaceae), *Doryanthes* (Doryanthaceae), and Tecophilaeaceae, are commonly placed close to Iridaceae in cladistic analyses (e.g., Chase et al., 1995; Rudall et al., 1997; Fay et al., 2000). Of these, the Australian bird-pollinated genus *Doryanthes* (ca. two spp.) is a good candidate for a sister group relationship with Iridaceae because it shares some synapomorphies, including presence of styloid crystals (and absence of raphides). Within Iridaceae, raphides are invariably absent and almost all taxa have styloids (Goldblatt et al., 1984) with the exception of *Sisyrinchium* and its close allies, which lack crystals altogether (a synapomorphy for this group: Rudall et al., 1986; Goldblatt et al., 1990). On the other hand, raphides are present (and styloids absent) in both *Ixiolirion* and Tecophilaeaceae (Prychid & Rudall, 1999). Furthermore, both *Doryanthes* and Iridaceae have extrorse anther dehiscence, a character that is otherwise unusual in Asparagales. *Ixiolirion* is a small Eurasian genus of ca. three species with epigynous flowers with septal nectaries in the top half of the ovary (Simpson & Rudall,

1998; Rudall, 2002). Fay et al. (2000) placed *Ixiolirion* with *Doryanthes* in an equally weighted multigene analysis and with Tecophilaeaceae in a successively weighted analysis. Analysis of morphological data (Rudall, 2002b) supported a close association between *Ixiolirion* and *Doryanthes*, although *Ixiolirion* shares a corm with Tecophilaeaceae (Kubitzki, 1998; Simpson & Rudall, 1998), while *Doryanthes* has a short vertical rhizome (Clifford, 1998).

Septal nectaries are absent from some Tecophilaeaceae (Simpson & Rudall, 1998), but present in both *Doryanthes*, in which copious nectar is secreted (Newman, 1928; Patil & Pai, 1981; Kocyan & Endress, 2001) and *Ixiolirion* (Rudall, 2002a). Loss of septal nectaries has apparently occurred *de novo* several times within Asparagales (Rudall, 2002a), including at least once in both Tecophilaeaceae and Iridaceae. Therefore, despite their absence from the putatively basal genus, *Isophysis* (see below, and introduction), the most likely scenario is that presence of septal nectaries is the plesiomorphic condition for Iridaceae (Fig. 1).

Total absence of septal nectaries (i.e., complete fusion of carpel margins) occurs sporadically within Asparagales (sensu APG, 1998), in contrast to the related order Liliales, where absence of septal nectaries and presence of perigonal nectaries both represent highly consistent synapomorphies (Rudall et al., 2000). Total absence of nectar often indicates an alternative pollination mode; for example, several asparagoid families with vibratile (buzz) pollination and *Solanum*-type flowers lack nectaries entirely, including some Laxmanniaceae (e.g., *Arthropodium*), some Hemerocallidaceae, some Tecophilaeaceae, and apostasioid orchids (Vogel, 1981; Dressler, 1993; Bernhardt, 1995, 1996; Kocyan & Endress, 2001; Rudall, 2001, 2002a). Septal nectaries are often absent from epigynous taxa (Rudall, 2002a) and always absent from "hyperepigynous" taxa with gynostemia such as Orchidaceae (Rudall & Bateman, 2002).

NECTARIES IN IRIDACEAE

Within Iridaceae, there is some topological conflict at the deeper nodes resulting from analyses of different data sets, especially between molecules and morphology, although even the molecular topologies differed in some respects (Reeves et al., 2001). Analysis of four plastid DNA data sets (*rbcL*, *rps4*, *trnL*, *trnL-F*) for 57 genera of Iridaceae plus outgroups, found that in each of the individual trees, some genera or groups of genera were misplaced relative to morphological cladistic studies,

but the combined analysis produced a tree in which all subfamilies were resolved as monophyletic, except that Nivenioideae formed a grade in which Crocoideae (Ixioideae) were embedded (Reeves et al., 2001). Among other genera of disputed affinities, *Geosiris* was placed within the nivenioid grade (Goldblatt et al., 1987), *Isophysis* was sister to the rest of the family, and *Diplarrhena* was placed in a well-supported position as sister to Iridoideae (Rudall & Goldblatt, 2001). *Bobartia* (formerly Sisyrinchieae: Goldblatt & Rudall, 1992) has found support as a member of Irideae (Iridoideae), by both Reeves et al.'s (2001) study and a molecular analysis of the ITS2 gene (Donato et al., 2000).

Assuming that the combined (successively weighted) molecular topology of Reeves et al. (2001) is correct, with the Tasmanian genus *Isophysis* as the basal taxon (Fig. 1), and also that the presence of septal nectaries is the plesiomorphic condition for Iridaceae (see above), then there are two possible evolutionary scenarios for this character within the family: (1) suppression of septal nectaries in the ancestor of Iridaceae plus at least two *de novo* developments of septal nectaries, in Nivenioideae/Crocoideae and *Diplarrhena* (and probably a subsequent secondary loss in Iridoideae), or (2) separate suppressions of septal nectaries in *Isophysis*, the basal Nivenioideae (*Aristea*, *Geosiris*, and *Patersonia*), and Iridoideae, as illustrated in Figure 1. The latter scenario would involve several separate losses of septal nectaries in *Isophysis*, *Aristea*, *Geosiris*, and *Patersonia*. However, it is possible that *Aristea*, *Geosiris*, and *Patersonia* may ultimately form a clade, since Reeves et al. (2001) suggested that the existing topology, which conflicts with morphological data for these taxa, is questionable due to high levels of sequence divergence. In any case, this hypothesis, although less parsimonious, is perhaps ultimately more plausible, especially if (as seems likely) perigonal nectaries evolved from septal nectaries (see below).

Nivenioideae and Crocoideae. The subfamily Nivenioideae is a relatively heterogeneous group with respect to several characters, including nectaries (Table 2). Reeves et al. (2001), in analyses of molecular data from four gene loci, found Nivenioideae to be paraphyletic to Crocoideae (Ixioideae), although the three shrubby Cape genera *Klattia* (3 spp.), *Nivenia* (10 spp.), and *Witsenia* (1 sp.) together formed a well-supported clade. *Klattia*, *Nivenia*, and *Witsenia* all have septal nectaries (Figs. 3A, F, G, 4D, E). In *Nivenia*, nectar ranges from 1 to 2 μl in volume, has a relatively high sugar concentration, and is sucrose-rich (Goldblatt, 1993). In contrast, nectar volumes in *Klattia* and

Witsenia are substantial; as much as 77.9 μl of nectar per flower has been recorded in *W. maura* Thunb. and 46.9 μl nectar in *K. stokoei* Guthrie (Goldblatt, 1993). In these genera nectar sugar concentrations are low, 12–15% sucrose equivalents, and nectars are hexose (glucose plus fructose)-dominant. Larger volumes of nectar, low sugar concentrations, and dominance of hexose sugars in these two genera are associated with sunbird pollination compared with anthophorine bee and/or long-proboscid fly pollination in *Nivenia* (Goldblatt, 1993).

Most species of the Afro-Madagascan *Aristea* (ca. 50 spp.; Nivenioideae) do not produce nectar and lack septal nectaries; the presence of perigonal nectaries in *A. spiralis* is apparently an autapomorphy for this species. *Aristea spiralis* is embedded within the derived subgenus *Pseudaristea*, which is characterized by derived large pollen grains with specialized 2-zonasulcate apertures (Goldblatt & LeThomas, 1997). Nectar production in *A. spiralis* appears to be correlated with its pollination by long-proboscid flies, evidently unique in the genus (Johnson, 1992; Goldblatt & Manning, 1997). Of the remaining genera of Nivenioideae, nectaries are absent from the Madagascan saprophyte *Geosiris*, and the salverform flowers of the Australasian *Patersonia*, which have a long perianth tube. In this genus the tube evidently serves to raise the nearly sessile flowers out of the long inflorescence spathes that enclose the flower buds.

Within subfamily Crocoideae (28 genera, currently arranged in three tribes), nectar characteristics are highly variable in volume and concentration, but are typically sucrose-rich to sucrose-dominant. This is associated with the diverse pollination systems found in most genera of the subfamily (Goldblatt et al., 1995, 1998, 2001, in press; Goldblatt & Manning, 2000; Bernhardt & Goldblatt, 2000). The only significant departure from the pattern of high sucrose concentration is in some (but not all) sunbird-pollinated species (Goldblatt et al., 1999, 2001). Discharge of nectar from septal nectaries is highly variable (Smets et al., 2000). Suppression of nectar production in some species of *Ixia* subg. *Ixia* is associated with a shift in pollination strategy from anthophorine bees to hopliine beetles in section *Ixia* (hopliines have no interest in nectar and use flowers largely as sites for assembly, mate selection, and copulation) (Goldblatt et al., 2000a). As far as is known, species of the other section *Dichone* of *Ixia* subg. *Ixia* are buzz pollinated by female anthophorine bees, and pollen is the sole floral reward (Goldblatt et al., 2000a). In subgenus *Ixia*, suppression of nectar secretion is correlated with the narrowing of the diameter of

the perianth tube so that its walls tightly surround the style. The tube in these species effectively functions as a stalk (pseudopedicel) for the outspread tepals. The narrowing of the tube so that it clasps the style occurs in species of several other genera, notably in *Romulea* and *Sparaxis*, but usually traces of nectar are still secreted and presented at the mouth of the tube (Goldblatt et al., 2000a, b), and de Vos (1972) has confirmed that septal nectaries are present in *Romulea*. Often, no trace of nectar can be detected in flowers of these species, presumably because the nectar has already been removed by visiting bees. In two species of *Hesperantha*, however, nectar secretion appears to be completely suppressed and pollination is accomplished by deceit, the flowers of these species resembling others that do secrete nectar (Goldblatt et al., in press).

In *Tritoniopsis parviflora*, production of floral oils from glandular epithelium at the base of the free parts of the tepals (Manning & Goldblatt, 2002) is apparently unique among Crocoideae. This species is pollinated over part of its range by the oil-collecting melittid bee, *Rediviva gigas*. Species of *Rediviva* are assumed to use floral oils as part of the food supply for larvae (Steiner & Whitehead, 1988, 1990).

Iridoideae: Diplarrhena.   The presence of septal nectaries in *Diplarrhena* argues against its inclusion in the subfamily Iridoideae, which otherwise entirely lack them. Rudall and Goldblatt (2001) erected a new tribe, Diplarrheneae, for this genus but noted that its phylogenetic position remains uncertain. Molecular data did not fully resolve the positions of either *Diplarrhena* or *Patersonia*, since they occupied reversed positions in the *rps*4 topology with respect to the *rbc*L and *trn*L-F trees (Reeves et al., 2001), although in the combined (successively weighted) molecular analysis their positions were strongly supported (BS > 96%) with *Diplarrhena* as sister to Iridoideae, and *Patersonia* sister to the remaining Nivenioideae/Crocoideae.

On the other hand, the presence of septal nectaries in Nivenioideae/Crocoideae plus *Diplarrhena* tends to support the *rps*4 topology (*Diplarrhena* as sister to Nivenioideae/Crocoideae) rather than the combined topology (Fig. 1), although *Diplarrhena* lacks the repeated codon of the *rps*4 gene that is found in the Nivenioid–Crocoid clade (Souza-Chies et al., 1997). *Diplarrhena* shares morphological similarities with some Nivenioideae; for example, pollen of *Diplarrhena* strikingly resembles that of *Patersonia*, both having distinctive inaperturate pollen with a vermiform surface patterning (Rudall & Goldblatt, 2001). Flowers of *Diplarrhena* differ from those of most other Iridoideae, especially in the style branches, which are flat lobes, unlike the tubular style branches (sometimes with apical appendages) and terminal or subterminal stigma lobes typical of Iridoideae.

Conversely, the leaf anatomy of *Diplarrhena* is rather similar to that of *Libertia* (Iridoideae–Sisyrinchieae) (Rudall, 1986, 1994), and the simple rhipidial inflorescences are consistent with those of other Iridoideae. Furthermore, although the subfamily Nivenioideae lacks clear synapomorphies and may well be paraphyletic (Reeves et al., 2001), *Diplarrhena* differs from them in some respects, notably inflorescence morphology, having flowers in simple rhipidia rather than the paired (or binate) rhipidia of all Nivenioideae (Goldblatt, 1990; Manning & Goldblatt, 1991). *Diplarrhena* also differs from Nivenioideae in that the root metaxylem vessels in all Nivenioid genera have only scalariform perforation plates, whereas in most other Iridaceae, including *Diplarrhena*, they are simple (Cheadle, 1963). Clearly, no single character can independently test relationships, and a revised morphological analysis of Iridaceae in the light of new data may help to resolve this conundrum.

Perigonal nectaries within Iridoideae.   Among other Iridoideae, there is apparently a preadaptation to production of perigonal secretory structures (character B in Fig. 1), since both perigonal nectaries and elaiophores (oil-producing glands) are widespread in the subfamily but otherwise unusual within Asparagales (although some Orchidaceae have nectariferous tepaline spurs).

The presence of sugary nectar (as opposed to oil) secreted from the filament column is an autapomorphy for *Olsynium*. The "diffuse" nectaries that occur in *Moraea lurida* and *M. ochroleuca* appear to be unique in the family, yet must have arisen independently from each other, since the two species belong in different subgenera (Goldblatt, 1986, 1998b). However, given their topological similarity and close phylogenetic relationship, it seems likely that the elaiophores found in some *Sisyrinchium* species may have evolved from perigonal nectaries.

Daumann's (1935) detailed work on nectaries in many different species of *Iris* (Iridoideae) may help to elucidate nectary evolution in Iridaceae. In some *Iris* species the nectariferous regions extend from around the base of the perianth/stamen tube and around the base of the style, so that the nectary exudes nectar at the same place as it would in an epigynous flower that possessed septal nectaries (e.g., in members of subfamily Crocoideae, or in *Dioscorea*, Dioscoreaceae: Caddick et al., 2000). This raises the intriguing possibility that perigonal

nectaries may have evolved from septal nectaries by heterochrony (temporal shifts), or possibly heterotopy (Alberch et al., 1979; Bateman, 1994; Baum & Donoghue, 2002; Rudall & Bateman, 2002), specifically reflecting later formation of nectaries that are expressed in a more distal position on organ primordia. This hypothesis, which requires testing in a molecular-developmental context, is dependent on taxa with perigonal nectaries having evolved from ancestors with septal nectaries (as shown in Fig. 1) rather than from taxa that lacked septal nectaries entirely. It is noteworthy that perigonal nectaries, which are relatively uncommon in monocots, are frequently associated with epigyny (e.g., in Iridaceae and Orchidaceae), although exceptions include some taxa of the order Liliales, in which perigonal nectaries are common and both epigyny and hypogyny occur (Rudall et al., 2000). Van Heel (1988) examined gynoecial and septal nectary development in some hypogynous Asparagales, but there have been very few such developmental studies on epigynous Asparagales, although Payer (1857) illustrated organogenesis in *Gladiolus communis* (Iridaceae) and Mogensen (1969) in *Agave* (Agavaceae). Rudall (2002a) examined floral development in the taxonomically isolated lower asparagoid genus *Xanthorrhoea* (Xanthorrhoeaceae), in which the ovary is hypogynous at anthesis but epigynous at early development stages, and septal nectaries are extensive. These investigations all showed initial free development of organ primordia (two peripheral tepal whorls, two stamen whorls, and finally three free carpels) and subsequent axial elongation of the receptacular/placental region by elongation of their common bases.

Furthermore, it seems unlikely that a *de novo* nectar source should have evolved in Iridaceae at the same time as suppression of septal nectaries, unless there is some developmental relationship between the two structures. Perigonal nectaries appear to be simply an alternative source of nectar for the same insects, including bees of various families, that also pollinate flowers of some Crocoideae, where nectar from septal nectaries is proffered. The absence or paucity of flowers adapted for specialized pollinators in Iridoideae, including long-proboscid flies, sunbirds, moths, and large butterflies, so common in Crocoideae, seems related to the presence of a well-developed perianth tube and widespread floral zygomorphy in Crocoideae and not directly to nectary type. However, the source of nectar is in the ovary, and thus at the base of the perianth tube where nectar is retained and beyond the reach of short-tongued or short-proboscid insects. This factor is obviously significant in the development of the specialized pollination strategies so common within Crocoideae (Bernhardt & Goldblatt, 2000).

It is also predictable that within Asparagales trichome elaiophores were exploited only in a subfamily in which perigonal nectaries were developed (i.e., Iridoideae). Oil collection is a widely exploited syndrome in the Neotropics and adjacent temperate zones to the north and south, and bees of several genera in different families utilize floral oils, hence the disproportionate development of oil secretion in the New and Old Worlds. In contrast to the situation in the New World, in which literally hundreds of Iridaceae secrete floral oils, in the Old World only one species of Iridaceae (*Tritoniopsis parviflora*) is known to do so, and only one genus of bees is adapted to exploit floral oil secretion.

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